

1918
B353

BIOLOGIC SPECIALIZATION IN THE GENUS
SEPTORIA

BY

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B. S. University of Minnesota, 1914.

M. S. Michigan Agricultural College, 1915.

THESIS

Submitted in Partial Fulfillment of the Requirements for the

Degree of

DOCTOR OF PHILOSOPHY

IN BOTANY

IN

THE GRADUATE SCHOOL

OF THE

UNIVERSITY OF ILLINOIS

1918

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UNIVERSITY OF ILLINOIS
THE GRADUATE SCHOOL

May 3, 1918

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY
SUPERVISION BY Walter Spurgeon Beach
ENTITLED Biologic Specialization
in the Genus Septoria

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR

THE DEGREE OF Doctor of Philosophy
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10-11-18

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BIOLOGIC SPECIALIZATION IN THE GENUS SEPTORIA

I Introduction

The genus *Septoria* presents an excellent field for the study of biologic specialization on account of the very large number and the uncertain status of the described species, of which there are more than 1200. The morphological characters for the limitation of these are few, consisting chiefly of spore shape, length, thickness, and septation, and in some instances a slight tinting of the spore; pycnidium shape, size, and color; and ostiole size and character. The biological characters for the limitation of species are the size, shape, margin, zonation, and color of the disease spots, and their location and distribution upon the host. The specific descriptions in many cases are meager and really useless. The presence of a *Septoria* upon an unrecorded host is often made the basis of a new species.

By tabulating (10), according to spore length, all the "species" of *Septoria* given in Saccardo's "Sylloge Fungorum", it has been found that nearly 700 fall within the limits of 20 to 50 microns. Twenty-six species on grasses are between 20 to 40 microns. Yet in one case a Saccardian description gives a spore length ranging from 19 to 62 microns. There have been great inaccuracies in measuring spores and pycnidia, with tendencies to report the measurements in round numbers. Elliott (7) has shown the degree of personal error with our modern technique. Among eleven observers measuring many spores of *Alternaria*, he found that there was a

variation of over 41% from the highest measurement returned for maximum length, and that such a variation would make it impossible to distinguish the species of *Alternaria* on the basis of spore measurement. Septation is largely dependent upon the stage of maturity of the spores, is often difficult to see, and was ignored by early mycologists. Environmental conditions cause fluctuations in the size of spores and pycnidia. The value of disease characters is doubtful for they commonly change with the age, the part, and the species of the host, as well as with weather conditions. The confusion that Cavara (4) met regarding these points in his attempt to distinguish *Septoria tritici* and *S. graminum* on wheat, led him to state that both forms probably belonged to the same morphological species.

Little is known respecting the existence of biologic specialization in the genus *Septoria*. Except for a few instances (15, 22, 45) no cross-inoculations have been made to ascertain whether a *Septoria*, as found upon a particular host, is restricted to that host, or is more or less cosmopolitan and adaptive in its parasitism. In the literature at present one is confronted by two extremes of treatment: (a) closely similar species are described on the same host, e.g., *Septoria lactucae* and *S. consimilis* on *Lactuca sativa*; (b) more widely variant forms on distantly related hosts are described as representing one species, e.g., *S. graminum* on twelve or more genera of grasses, and a species of sedge. It is obvious that such practice is not consistent, and cannot adequately reflect the truth.

The facts as presented above are illustrative of the present unsatisfactory status of the species not only of *Septoria* but also

of many other genera of the Fungi Imperfecti. More accurate knowledge regarding host characters, morphological variation, and biological specialization is greatly needed from the standpoint of classification. The genus is the more worthy of study on account of its high economic importance. To study such a large genus as *Septoria* in culture, either upon the living hosts or upon artificial media, would require the time of many investigators. The present paper is intended merely as a contribution to the general problem as suggested above, and the investigations were conducted with the following leading objects:

1. to determine the host range of as many species of *Septoria* as possible in order to ascertain; (a) whether morphologically similar forms from different hosts vary in host range, (b) whether morphologically unlike forms ever have the same host range; or in other words to ascertain whether any of the species available for study consist of a number of biological forms, and whether any now listed as distinct species are identical.

2. to compare disease characters, i.e., the host response to infection, when produced (a) by a single species of *Septoria* upon dissimilar hosts, or (b) by different species of *Septoria* on the same host.

3. to note any morphological changes in the size and shape of spores and pycnidia as a result of change of host or of the condition of the host, or of other environmental factors.

4. to determine the susceptibility of different parts of the same host and of these at different stages of maturity, and to note whether any distinctions in disease characters are correlated with host structure and condition.

II Historical

The literature dealing with biologic specialization is extensive. A comprehensive review cannot be undertaken here, yet a brief summary of the essential points, especially as brought out by the investigations of rusts and powdery mildews, will be useful in the interpretation of results to be presented. It may be well to mention that biologic specialization is also spoken of as "adaptive parasitism", and biologic forms as "biologic species", "biologic races", "physiological races", and "adapted races."

While Eriksson was first to conduct extensive experimental work in biologic specialization, the idea was in the minds of earlier investigators for Schröter (8, footnote) in 1879 spoke of splitting up the old species Puccinia caricis into a number of forms differing slightly morphologically, but widely in biologic characteristics.

Eriksson (8) called attention more definitely to the nature of biologic specialization through the results of his cross-inoculation experiments with Puccinia graminis in Sweden. He found that, although this rust upon the cereals and grasses represented the same morphological species, the form upon one host-species was not always identical with the form upon another; since, for example, oat rust would transfer to oats, but not as a rule to other species of Gramineae. He showed that this fungus embraced at least six distinct forms distinguished by their dissimilar powers of infection with respect to the species of the grass family. In a subsequent paper (9) Eriksson showed that the trend of specialization may be different in isolated localities. This was illustrated by the fact that the form on rye, Puccinia graminis secalis, has a

relatively vigorous development in Sweden, but a relatively weak one in North America. In the case of Puccinia graminis tritici on wheat the more vigorous development is in the latter country.

Hitchcock and Carleton (13) performed early infection experiments with Puccinia graminis in the United States, and obtained results in agreement with those of Eriksson. Carleton (2,3) in working with biologic forms of rusts has secured valuable data upon varietal resistance in cereals.

Ward (46), experimenting with Puccinia dispersa upon *Bromus*, showed the presence of several biologic forms of this fungus on this single host-genus, and discovered "bridging species". The nature of a "bridging species" is described by this statement of the author: "although it is generally true that the adapted races of Puccinia dispersa are restricted to groups of closely allied species, there do occur species which serve as intermediaries in the passage of the fungus from one section of the genus to the other."

Arthur (1) reported that Puccinia helianthi is divided into a number of biologic races, and that Helianthus annuus acts as a bridging host.

Stakman (42) in a study of the physiological races of rusts showed that the power of wheat rust to infect rye was somewhat increased when the fungus lived a number of generations on barley.

Recently Stakman and Piemeisel (43) have published the results of extensive infection experiments with Puccinia graminis from 35 species of native grasses collected in widely separated regions of the Northwestern States. More than one biologic form was found to occur on the same host in nature. It was necessary

to employ differential hosts to determine the identity of the forms. These authors claim, moreover, that the biologic forms of Puccinia graminis can be distinguished from one another morphologically as well as biologically, by the size, shape, and color of the urediniospores. Regarding susceptibility they state, "all gradations in susceptibility occur from complete immunity to complete susceptibility to the various biologic forms. The following reactions may be made to inoculation: no visible effect, appearance of small flecks, production of very small uredinia without flecks, production of very small uredinia in small or large flecks, production of large uredinia surrounded by small dead areas or by apparently healthy tissue."

With the Erysiphaceae the extension of our knowledge of biologic specialization has had a similar course. Although Salmon had discussed the probable existence of biologic specialization in this group of fungi, Neger (21) was first to report definite data. Neger said that Erysiphe cichoracearum would not cross-infect among certain of the numerous hosts of this mildew.

Marchal (17) soon followed Neger with a paper describing seven "formes spécialisées" in the Oidium of Erysiphe graminis, and said each was confined to a single genus of grasses or cereals.

Salmon then attacked the problem of adaptive parasitism in the powdery mildews, and published a long series of papers (1903-1906). His important work concerns the Oidia on *Bromus* and *Hordeum*. He proved that several biologic forms of the Oidium parasitized the species of *Bromus*, that an individual species may be the meeting place of several biologic forms, and that "bridging species" existed. An additional discovery is best stated in his

own words, (35,p 57) "the inter-relations of the biologic forms with certain of their host-plants become complicated by the existence of 'biologic forms' of the host plants." Salmon found that in Bromus mollis there was a susceptible and an immune race with respect to four separate biologic forms of the mildew. In his study of the various kinds of cultivated barleys (32), he was able to arrange the varieties in a series according to their susceptibility. In experiments with ascospores (31,37) he found that adaptation in the perfect stages of Erysiphaceae is parallel to that in the conidial.

Salmon made histological studies (38) to see what development the mildew reached when sown upon non-susceptible leaves. He discovered that the germ tube of the conidium penetrated the epidermal cell and sometimes formed an incipient haustorium within, but that further development was usually arrested, indicating that resistance was a physiological factor of the cell contents, and not morphological. He showed (39) that resistance to a biologic form can be overcome by injuring the host, or by treating it with certain narcotic vapors.

G. M. Reed has been the chief worker in the United States upon adaptive parasitism in the powdery mildews, and has published numerous papers (1905-1916). In addition to corroborating the results of Salmon and others, he has carried out extensive cross-inoculation experiments with Erysiphe graminis (27,28,29) in which he has shown considerable variation in susceptibility among the species and varieties of Triticum, Hordeum, Avena, and Secale, a few of which are immune. In Erysiphe chicoracearum (25) on Cucurbitaceae he found but one biologic form, capable of growing upon various members of this host-family.

The more important instances of biologic specialization reported in other groups of fungi are as follows: by Stager in *Claviceps* (41), by Diedicke in *Pleospora* and its conidial stage *Helminthosporium* (5), by Gilbert in *Plowrightia morbosa* (11), by Müller in *Rhytisma acerinum* (20), and by Hesler in *Sphaeropsis malorum* (12). Shear and Wood (40) found that the races of *Glomerella cingulata* from different hosts varied somewhat in the vigor of their attack upon other hosts. Tests by Westerdijk (47) indicate the absence of biologic specialization among similar races of *Sclerotinia libertiana*. Rands (23) has proven by cross-inoculation that the *Alternarias* of *Datura* and potato are not identical as some have supposed.

With species of *Septoria* only a few investigators have worked. Levin (15) inoculated several plants akin to the tomato with *Septoria lycopersici*. Definite small black spots without pycnidia appeared on potato, but no effect was seen in other plants. Norton (22) performed similar experiments in humid inclosures, and obtained infection upon several species of *Solanum*. A further discussion of this author's results will be given in a subsequent section. Stone (45) proved by infection that *Septoria ribes* and likewise its perfect stage *Mycosphaerella grossulariae* taken from *Ribes nigrum* will infect *R. grossularia*, *R. rubrum*, and *R. oxycanthoides*.

Montemartini (18) has concluded that parasitic fungi are extremely sensitive to the chemical composition of the nutritive medium on which they live, and under its influence acquire characters of adaptation which attain to a certain fixity. In consequence fungi may become unable to flourish on species different

from those to which they have accustomed themselves, or even on other portions of the same plant which they inhabit, or in different developmental stages of such plant or organ. This problem is further complicated by atmospheric conditions, and the influence thereof upon sensitivity to attack as well as upon the virulence of the infecting bodies.

The review as here given serves to illustrate the intricate nature of biologic specialization, and to remind one of the various factors to be considered in the interpretation of the results of inoculation experiments.

III Experimental Methods and Material

The species of *Septoria* for investigation were with few exceptions collected in the vicinity of Urbana, Illinois. During the growing season spore-bearing material was gathered in the field from naturally infected plants. Leaves with disease spots were usually placed in a moist chamber for a day to cause heavy sporulation. In fall and winter spores were obtained in most cases from pure cultures isolated before the first frost. None of the cultures appeared to lose virulence, and it was found that this was the most certain way to keep infection material in readiness. In preparation for inoculation, spore suspensions were made with distilled water and were concentrated enough to contain fifty to one hundred spores per loop.

The experiments were begun in June and were continued to the following April. In summer the work was conducted in the field upon plants growing in their natural state. Freedom from disturbance and as far as possible from natural infection governed the selection

of suitable individuals. After the first frost the experiments were continued in the greenhouse upon potted plants transplanted from nature or grown from seed.

The method of inoculation was somewhat varied. In the field an atomizer was most convenient for the spore suspension could be carried safely in the glass container. In the greenhouse a wire loop was more commonly used to spread drops of the suspension over the leaf surface. Where a bloom or other epidermal structures made it difficult to secure good contact, especially with leaves of grasses, the suspension was rubbed on with the clean finger tips with proper care. Consistency of method was followed in a single series to secure comparable results. The entire surface of certain leaves was inoculated, while adjacent leaves of the same plant or near plants were used as checks to detect foreign infection where there was danger of this. Inoculations were made upon individuals of the original host to afford a check upon the viability of spores, or upon unfavorable environmental conditions.

Some difficulty was experienced in providing conditions favorable for infection. At first bell jars were placed over the plants for the customary period of two days, but later it was found better to vary this from three to five days. Paraffined paper bags were subsequently substituted for bell jars as they were more convenient to handle in the field, and gave more uniform results, possibly because they provided partial shade. The use of these bags was continued in the greenhouse. In cases in which disease spots without pycnidia resulted, the bags were replaced over the plants for a second period to promote the growth of the fungus, and to induce if possible the development of spore-bearing bodies. If this failed

the spotted leaves were detached and put into a sterile moist chamber. In this manner pycnidia were obtained and infection proven in some cases in which results would otherwise have been in doubt. This was especially necessary in instances in which spore suspensions were made from natural material, and the spores of other fungi might have been present to cause the spots.

In the following accounts the results of the inter-inoculations with each species of *Septoria* are presented graphically by means of diagrams, and in more detail by means of tables. The arrows in the diagrams indicate infection, and the lines ending in bars non-infection. The denominators of the adjacent fractions state the total number of leaves inoculated, and the numerators the number of leaves having one or more infected spots. The total number of spots formed is given in the tables where this is required for a closer comparison of susceptibility. In column two of the tables the letter f indicates that the experiment was in the field or out of doors, and g in the greenhouse. The letter b with the accompanying figure records the number of days the plant was bagged immediately following inoculation.

The lists of hosts given were compiled partly from Saccardo's "Sylloge Fungorum", and partly from data furnished by the herbariums at the New York Botanical Garden, and in the United States Department of Agriculture.

IV Septoria polygonorum Desm.

All the collections of Septoria made from species of Polygonum at Urbana were determined as Septoria polygonorum Desm. This fungus has been reported upon the following species of Polygonum, which are arranged in groups:

A. Infected by author

P. persicaria
" pennsylvanicum
" lapathifolium
" orientale

B. Inoculated but not infected

P. amphibium
" hydropiper
" convolvulus

C. Unused in experiments

P. bistorta
" sieboldii
" mitis
" hydropiperoides
" muhlenbergii
" dumetorum

D. Synonymous

P. incarnatum = P. lapathifolium
" nodosum = " "

The members of group C are foreign, or were not found growing in this vicinity. The species of group B, as well as others that gave negative results when inoculated, apparently had sufficient opportunity to become infected in nature; for infected plants of smartweed were usually growing in close proximity to the uninfected kinds. Yet repeated search for material resulted in finding Septoria polygonorum upon only Polygonum persicaria, P. pennsylvanicum, and P. lapathifolium, upon which the form in this locality appears to be specialized. The plants of P. orientale were few and apparently escaped infection by being isolated. It remains an open question whether the forms of S. polygonorum reported upon P. amphibium, P. hydropiper, and P. convolvulus of group B are differently specialized or whether the hosts are resistant in this region. The former case is likely if the fungi and their hosts were correctly determined.

With respect to the power of the fungus on one species of group A to infect the other susceptible species, there appears no certain distinction among the Septoria forms from these hosts, at least in the light of the limited number of experiments. On July 10 (table I) a plant each of P. pennsylvanicum and P. persicaria growing together in a shaded place was inoculated with spores from P. persicaria. Heavy infection resulted in the latter, while P. pennsylvanicum remained uninfected. Had there been previous natural infection, it is very improbable that the plant of P. pennsylvanicum should have escaped it, for the branches of the two specimens almost interlocked. Thus it seems that this individual of P. pennsylvanicum was resistant. On Oct. 3 this experiment was repeated upon a plant of P. pennsylvanicum that had been watched under a bell jar for previous infection. This specimen gave full infection with spores from P. persicaria.

Septoria polygonorum was isolated, and the growth characters were alike in the fungus as isolated from each of the four hosts in group A.

Although a vigorous parasite upon the few species of Polygonum, the form of Septoria polygonorum dealt with here is not at all cosmopolitan in its parasitism. A special attempt was made to infect a plant of P. convolvulus kept constantly covered with a paraffined paper bag to insure a humid atmosphere and provide partial shading, but with negative results. One hundred leaves of P. hydropiper also gave negative results. The fungus was induced to attack detached leaves of P. convolvulus kept in a moist chamber in the warm laboratory, spots and pycnidia developing in seven days; but it would not attack Rumex crispus or Fagopyrum esculentum in a

Table I

Infections with Septoria polygonorum Desm.

Date	Condi- tions	Plants inoculated	No. of leaves infected & inoculated	No. of spots	Check in- fections on original host
Spores from <u>Polygonum pennsylvanicum</u>					
June 28	f-b 2	<u>Polygonum persicaria</u>	12/16	many	8/10
Aug. 30	f-b 2	" "	11/20	many	
Sept. 6	f-b 3	" "	8/12	45	
Sept. 14	f-b 3	" "	10/15	26	
			41/63		
Aug. 30	f-b 4	<u>Polygonum lapathifolium</u>	3/10	34	
Sept. 14	f-b 4	" "	5/5	many	6/6
			8/15		
Sept. 14	f-b 4	<u>Polygonum orientale</u>	6/6	28	6/6
June 9	shaded	<u>Polygonum erectum</u>	0/10		4/5
June 28	f-b 3	" "	0/11		8/10
			0/21		12/15
June 28	f-b 0	<u>Polygonum convolvulus</u>	0/8		8/10
June 28	shaded	<u>Polygonum hydropiper</u>	0/45		8/10
Sept. 7	shaded	<u>Polygonum acre</u>	0/12		
Sept. 21	f-b 4	" "	0/20		plus
			0/32		
Sept. 21	shaded	<u>Polygonum scandens</u>	0/25		plus
June 28	shaded	<u>Polygonum amphibium</u>	0/7		8/10
Spores from <u>Polygonum persicaria</u>					
July 10	shaded	<u>Polygonum pennsylvanicum</u>	0/10		10/15
Oct. 3	g-b 5	" "	5/5	many	
			5/15		
Sept. 9	f-b 4	<u>Polygonum lapathifolium</u>	7/10	many	10/10
Sept. 20	f-b 4	<u>Polygonum orientale</u>	7/7	many	
July 10	shaded	<u>Polygonum convolvulus</u>	0/20		10/15
Mar. 3	g-b 3	" "	0/5		
			0/25		
July 10	shaded	<u>Polygonum hydropiper</u>	0/30		10/15
Sept. 28	f-b 4	" "	0/25		plus
			0/55		
July 10	f-b 3	<u>Polygonum erectum</u>	0/25		10/15

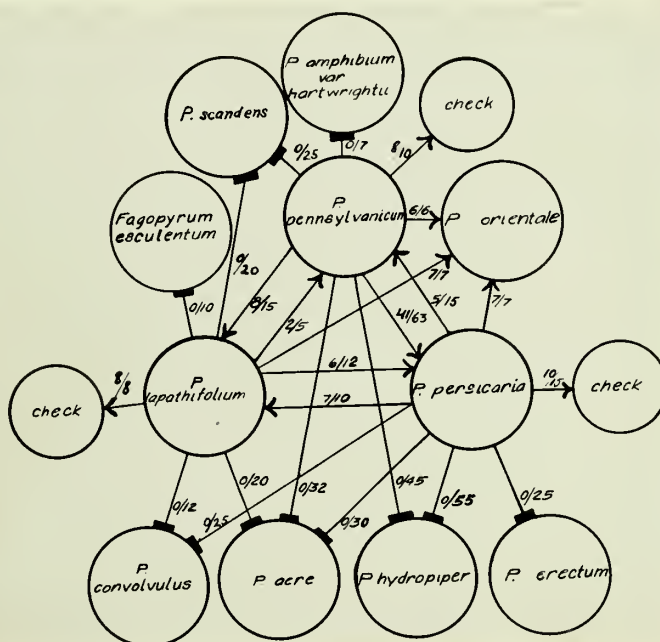
Infections with Septoria polygonorum Desm.

Sept. 7	shaded	Polygonum acre	0/10		
Sept. 22	f-b 4	"	0/20		
			0/30		

Spores from Polygonum lapathifolium

Sept. 11	f-b 3	Polygonum pennsylvanicum	2/5	15	
Sept. 21	f-b 3	Polygonum persicaria	6/12	15	8/8
Mar. 10	g-b 3	"	3/4	13	
			9/16	28	
Sept. 21	f-b 3	Polygonum orientale	7/7	many	8/8
Sept. 21	f-b 4	Polygonum hydropiper	0/25		8/8
Sept. 21	f-b 4	Polygonum acre	0/20		8/8
Sept. 21	shaded	Polygonum scandens	0/20		8/8
Oct. 7	g-b 4	Polygonum convolvulus	0/12		
Dec. 3	moist chamber	Polygonum convolvulus (leaves detached)	3/7		
Oct. 7	g-b 4	Fagopyrum esculentum	0/10		
Dec. 3	moist chamber	Fagopyrum esculentum (leaves detached)	0/7		
Dec. 3	moist chamber	Rumex crispus (leaves detached)	0/7		

Diagram I.
Infection with Septoria polygonorum from Polygonum pennsylvanicum, P. persicaria, and P. lapathifolium



similar way. Thus Septoria polygonorum appears as a species with fairly fixed infection-powers, possibly embracing forms differently specialized in addition to the one experimented with here.

The disease spots are not the same on the various species of Polygonum. The distinctions are illustrated in Plate I, Figs. 1-4. The specimens were selected as representing the usual character of the spots. Specimens of the same species might have been selected showing scarcely distinguishable spots. Upon P. pennsylvanicum the spots attain the greatest size, often become irregular in outline, have but a very narrow, dark-brown border, and have pycnidia uniformly distributed throughout their area (Fig. 1). The spots upon P. persicaria are intermediate in size, and are chiefly characterized by a rather wide, dark reddish-brown border. The spots seldom lose their orbicular shape, and the pycnidia are grouped nearer the center (Fig. 2). Upon P. lapathifolium the spots range smallest in size, and are yellowish-brown in the fresh leaves, with a border of the same color, but in the dry specimens the spots become reddish-brown (Fig. 3). In size and shape the spots on P. orientale resemble those on P. pennsylvanicum, but are yellowish-brown in the fresh leaf. The reddish-brown border appeared when the leaf was put into a moist chamber for a day. The variability in the biological or host characters shown here illustrates the untrustworthy nature of these characters when used to distinguish species.

V Septoria lactucicola E. & M.

The plants inoculated with Septoria lactucicola were grown in pots in the greenhouse. Some had been grown from seed, others had

been transplanted from the field. As a rule only young or recently mature leaves were sown with spores. The spore material was obtained from the field.

Septoria lactucicola has been reported upon Lactuca floridana, L. scariola, and L. canadensis, but in most instances on the last plant. The results in Table II show that this Septoria is somewhat adaptive in its parasitism, being able to attack three genera and five species. Were the experiments conducted on a broader scale the host range would probably be enlarged. There is a gradation in susceptibility passing from L. canadensis through to Sonchus oleraceus. Although the fungus attacked L. sativa and L. scariola rather readily, with 18 spots on 30 leaves and 10 spots on 35 leaves respectively, the infection was slight compared with 23 spots on 7 leaves of the original host. Moreover, there were but few fruiting bodies on these new hosts. The most of the 17 spots on Prenanthes sp. were very small, and Sonchus oleraceus was a very uncongenial plant for the fungus. The comparison will be more clear with a description of the spots.

Septoria lactucicola produces upon L. canadensis round, reddish-brown to black spots, usually from 3 to 15 mm. in diameter, and frequently with concentric zones of lighter and darker color. L. scariola was the only new host in which these characters were preserved, and here the spots were lighter colored, probably on account of the thinner leaves. Upon L. sativa the spots were spreading, with an indefinite border, and several times larger than those on L. canadensis where the border is very definite. They were colored light brown in the center, gradually changing to yellow and then to the green of the normal tissue. No pycnidia were observed

Table II

Infections with Septoria lactucicola F. & M.
from Lactuca canadensis

Date	Condi- tions	Plants inoculated	No. of leaves infected & inoculated	No. of Spots	Remarks
Oct. 2	g-b 4	Lactuca canadensis	4/6	many	Check
Oct. 26	g-b 4	" "	5/7	23	"
			9/13		
Oct. 26	g-b 4	Lactuca sativa	10/30	16	Pycnidia few
Oct. 26	g-b 4	Lactuca scariola	6/35	10	Pycnidia few
Oct. 2	g-b 3	Prenanthes sp.	2/8	3	Spots small
Oct. 26	g-b 4	" "	1/10	4	" "
Nov. 15	g-b 7	" "	4/8	10	" "
			7/26	17	
July 11	g-b 4	Sonchus oleraceus	2/6	3	Pycnidia in
Aug. 30	g-b 3	" "	1/4	2	moist cham-
Oct. 2	g-b 4	" "	2/5	2	ber
			5/15	7	
Oct. 2	g-b 4	Sonchus asper	0/25		
Oct. 26	g-b 3	" "	0/40		
			0/65		
Oct. 2	g-b 4	Sonchus uliginosus	0/3		
Oct. 26	g-b 4	" "	0/8		
			0/11		
Oct. 2	g-b 5	Taraxacum officinale	0/8		
Oct. 26	g-b 5	" "	0/14		
			0/22		

in the greenhouse, but they developed in two days upon leaves detached and put into a moist chamber. For a further comparison of the spots on these first three hosts compare Plate I, Figs. 7-9. The spots upon Prenanthes sp. were 1 mm. to 3 mm. in diameter, dark brown, more or less angular, and usually surrounded by a greenish-yellow zone. Pycnidia were seen upon the plant, but spores developed only in the moist chamber. The spots upon Sonchus oleraceus were 1 mm. to 5 mm. in diameter, grayish brown, and more or less limited by the leaf veins. A small number of pycnidia with spores characteristic of Septoria lactucicola were obtained upon two of several infected leaves placed in a moist chamber.

That the biologic characters change with the host is clearly shown. Such variation has doubtless led to erroneous determinations or to the useless multiplication of species in many instances. Environment may likewise cause alterations of these characters for the spots on L. canadensis tended to lose their concentric zones and become spreading if kept long in a moist atmosphere.

VI Septoria lactucae Pass.

The following hosts are reported for Septoria lactucae: Lactuca sativa, L. scariola, L. virosa, L. canadensis, and Chondrilla muralis. The fungus appears to cross readily between L. sativa and L. scariola, and causes upon both of these hosts marked disease. The passage of the fungus from either of these hosts to L. canadensis apparently takes place only under very favorable conditions of heat and moisture, for it was necessary to cover the plants for a prolonged time with bags, and to atomize them

frequently with water to secure infection. A considerable degree of infection was secured in this way, yet it is probable that this *Septoria* does not occur commonly on *L. canadensis* in nature. The disease characters on *L. canadensis* were different from those seen upon *L. sativa* or *L. scariola* as the spots were smaller, had no tendency to spread, were darker in color, and commonly had a yellow zone for a border. They were angular in outline, usually 1 mm. to 5 mm. broad, and the central area was brown to black. Pycnidia and spores were present.

Especially favorable conditions were also provided in order to infect *Sonchus asper*, still the transfer of the fungus to this more distantly related host was not difficult for more than 25% of the inoculated leaves were more or less diseased. Such infection raises a question of identity between *Septoria lactucae* and certain of the species of *Septoria* described upon the genus *Sonchus*. An examination of exsiccati showed a close similarity between *S. lactucae* and *S. sonchifolia*, but more extensive data are needed to prove their identity. The spots formed upon *Sonchus asper* by *S. lactucae* were grayish-brown to black, angular in outline, 1 mm. to 5 mm. in width, and contained reproductive bodies.

If *Septoria lactucae* is compared with *S. lactucicola*, it is found that the two species are different in their adaptation to their hosts as well as being different morphologically, although the host ranges of the two almost coincide. Each infects *Lactuca sativa*, *L. scariola*, *L. canadensis*, and can pass over to the genus *Sonchus*. Yet *S. lactucae* is best adapted to *L. sativa* and *L. scariola*, grows less readily upon *L. canadensis*, and infects *S. asper* somewhat, while *S. lactucicola* is best adapted to *L. canadensis*

grows less readily upon L. sativa and L. scariola, and infects S. oleraceus slightly.

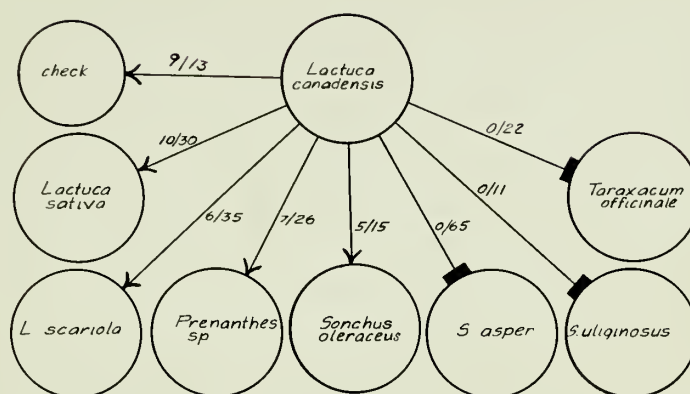


Diagram II. Infections with Septoria lactucicola from Lactuca canadensis.

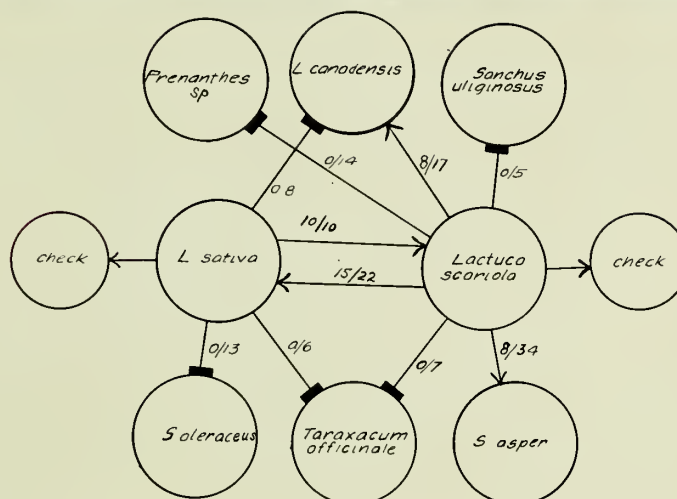


Diagram III. Infections with Septoria lacticae from Lactuca sativa and Lactuca scariola.

Infections with Septoria lactucae Pass.
from Lactuca sativa and Lactuca scariola

Date	Condi- tions	Plants inoculated	No. of leaves infected & inoculated	No. of spots	Remarks
Original host <u>Lactuca sativa</u>					
July 11	f-b 0	<u>Lactuca scariola</u>	10/10	many	Spots like those on this host in nature
Sept. 6	g-b 3	<u>Lactuca canadensis</u>	0/4		
Feb. 10	g-b 3	" "	0/4		
			0/8		
Sept. 6	g-b 3	<u>Sonchus oleraceus</u>	0/6	few	Small spots but
Feb. 10	g-b 3	" "	0/7		no pycnidia
			0/13		
Sept. 6	g-b 2	<u>Taraxacum officinale</u>	0/6		
Original host <u>Lactuca scariola</u>					
July 11	f-b 0	<u>Lactuca sativa</u>	5/12	10	Spots like those
Mar. 2	g-b 3	" "	10/10	75	on this host in
			15/22	85	nature
July 11	g-b 4	<u>Lactuca canadensis</u>	0/5		Spots brown to
Mar. 2	g-b 7	" "	8/12	53	black and rela-
			8/17		tively small
July 12	g-b 3	<u>Sonchus asper</u>	0/8		
Nov. 11	g-b 3	" "	3/6		Pycnidia and
Mar. 2	g-b 5	" "	5/20		spores
			8/34		
July 20	f-b 0	<u>Prenanthes sp.</u>	0/6		
Nov. 11	g-b 4	" "	0/8		
			0/14		
Nov. 11	g-b 4	<u>Sonchus uliginosus</u>	0/5		
Nov. 11	g-b 4	<u>Taraxacum officinale</u>	0/7		

VII Septoria tritici Desm.

There was some uncertainty regarding the name of the species of *Septoria* from wheat used in these experiments. In the literature two species are frequently mentioned as associated on Triticum vulgare; viz, Septoria tritici Desm., described in 1842, and S. graminum Desm., described in 1843. To the latter is usually ascribed the damage done to winter wheat and other cereals by *Septoria*. Cavara (4,p.21) in studying the forms of *Septoria* on wheat was confronted by so much disagreement that he revised the descriptions of Desmazières as follows:

" Die Septoria tritici Desm. (Pl. Cryptog. no. 669), welche anfangs gelbe, dann rostbraune, und endlich weissliche Flecke durch die Zerstörung des Parenchyms bildet, hat gewöhnlich gefächerte Sporen von 50 bis 60 x 1.5-2 μ ; sie sind von fadenförmiger Gestalt mit häufig ein wenig aufgetriebener Mitte. Die Scheidewände sind von Desmazières nicht bemerkt worden.- Die Septoria graminum Desm. (Pl. Cryptog. no. 728) besitzt Perithechien die dem blossen Auge nicht wahrnehmbar und kleiner und dichter gestellt als bei der vorigen Art sind; sie bilden durch ihre Vereinigen längliche grau nebelige Flecke. Die Sporen sind etwas feiner als bei Septoria tritici und ein Ende ist dicker als das andere; sie messen 40-50 X 1-1.5 μ , sind nicht gefächert, zeigen aber mehrere Tröpfchen."

Upon the basis of this revision Cavara compared all the exsiccati specimens available to him. His comparisons led him to make this statement: (4, p.22) " Wenn man sich nun Rechenschaft

von der grossen Veränderlichkeit der Charaktereigenschaften giebt, wie Form und Farbe der Flecke, Grösse der Perithechien, Vorhandensein or Fehlen der Scheidewände bei der Gattung Septoria, so wird es sehr wahrscheinlich das *S. graminum* und *tritici* ----- nur Formen einer einzigen mycologischen Art sind und die sich ergebenden Differezen vielleicht nur der Verschiedenartigkeit der Wirtspflanze zuzuschreiben sind"

The collections of *Septoria* from wheat used in the present investigation were made from one plot of Turkey Red winter wheat at the Illinois Experiment Station. In June, at a time when the grain had fully headed, nearly all the leaf blades were more or less infected. After harvest volunteer clumps of wheat came up from heads scattered on the ground, and in October the leaves in these clumps were badly attacked by *Septoria*. Collections for purposes of inoculation were made at this time, and also in December and January. After the ground froze the clumps were cut out, allowed to thaw slowly, and were then kept in a closed collecting can in the greenhouse. In a few days the pycnidia were forming spores abundantly.

The spores from the above source, collected either in summer or winter, were septate, and the pycnidia were brownish-black, round to elliptical when viewed from above, usually arranged in rows between the leaf veins, and were often visible to the naked eye. The spores from the leaves of the plants that had been frozen and then treated as mentioned were much longer but somewhat more slender than spores from material collected in other ways. Septation was difficult to detect, and seemed to be absent in some cases, but proper staining made it apparent in the most of the

Table IV
Infections with *Septoria tritici* Desm.
from Triticum vulgare

Date	Condi- tions	Plants inoculated	No. of leaves infected & inoculated	Remarks
Oct. 23 Jan. 19	g-b 3	<i>Triticum vulgare</i> (var. turkey red)	45/53 30/55 <u>75/108</u>	Check "
Oct. 23	g-b 3	<i>Triticum vulgare</i> (var. home grown spring)	46/48	
Dec. 28 Jan. 19	g-b 4 g-b 4	<i>Triticum dicoccum</i> " "	0/20 0/20 <u>0/40</u>	Leaves blanched " "
Jan. 19	g-b 4	<i>Triticum compactum</i>	0/10	Leaves blanched
Jan. 19	g-b 4	<i>Triticum polonicum</i>	0/12	Leaves blanched
Dec. 28 Jan. 19	g-b 4 g-b 4	<i>Triticum durum</i> " "	0/20 0/20 <u>0/40</u>	Leaves blanched
Oct 23 Jan. 19	g-b 3 g-b 4	<i>Secale cereale</i> " "	0/25 0/35 <u>0/60</u>	
Oct. 23 Jan. 19	g-b 3 g-b 4	<i>Hordeum vulgare</i> " "	0/27 0/30 <u>0/57</u>	Leaves blanched
Oct. 23 Jan. 19	g-b 3 g-b 4	<i>Avena sativa</i> " "	0/28 0/30 <u>0/58</u>	Leaves blanched " "
Oct. 23 Jan. 19	g-b 3 g-b 4	<i>Agropyrum repens</i> " "	0/21 0/9 <u>0/30</u>	
Oct. 23	g-b 3	<i>Poa pratensis</i>	0/17	
Oct. 23	g-o 3	<i>Phleum pratense</i>	0/30	
Oct. 30	g-b 3	<i>Festuca elatior</i>	0/30	
Oct. 23 Jan. 19	g-b 3 g-b 4	<i>Dactylis glomerata</i> " "	0/15 0/15 <u>0/30</u>	

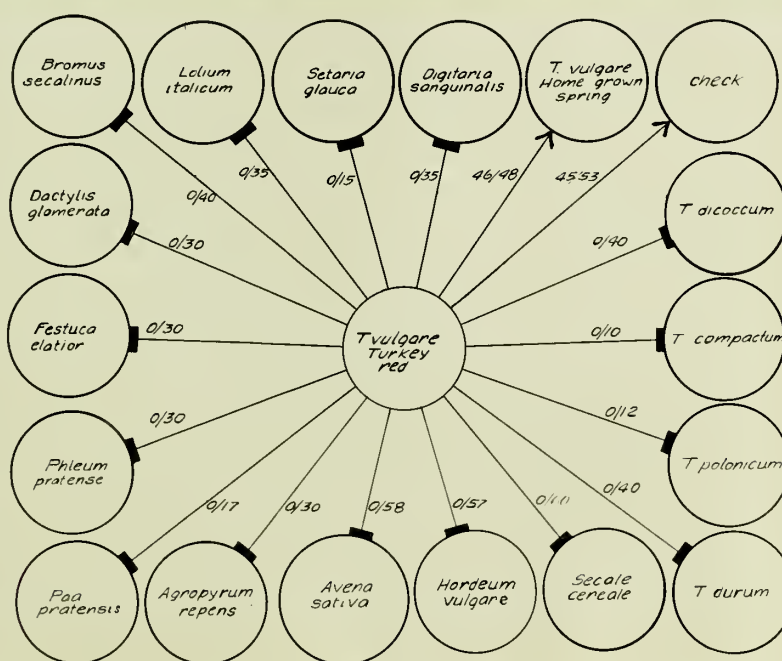
Table IV continued

Infections with Septoria tritici Desm.from Triticum vulgare

Oct.23	g-b 3	Bromus secalinus	0/40	
Oct.23	g-b 3	Lolium italicum	0/35	
Jan.19	g-b 4	Setaria glauca	0/15	
Oct.23	g-b 3	Digitalis sanguinale	0/35	

Susceptibility of
varieties

Jan.19	g-b 4	Turkey Red	30/55	Spots large with numerous pycnidia
" "	g-b 4	Beloglina	26/50	As above
" "	g-b 4	Pesterboden	23/54	Spots intermediate in size, pycnidia few
" "	g-b 4	Malakoff	28/65	As above
" "	g-b 4	Hungarian	8/32	Spots few and small with very few pycnidia

Diagram IV. Infections with Septoria tritici
from Triticum vulgare

spores. The pycnidia under these same conditions were often more than double their ordinary size, but were unchanged in shape. Infections obtained upon wheat seedlings by inoculation with these longer types of spores always resulted in pycnidia of normal proportions, and in shorter spores with more definite septa, typical of the fungus found on the leaves of wheat in summer or fall. A more comprehensive description of these morphological variations will be given in a subsequent section.

Whether one base his conclusions upon Cavara's revised descriptions, or upon his assertion that Septoria tritici and S. graminum are probably identical, the fungus at hand must be designated S. tritici Desm., in one case on account of morphology, and in the other on account of priority. Yet circumstances indicate that the organism is the same as that often reported as injuring wheat and other cereals and called S. graminum. (4,14,16,19). It is well to note, however, that all the inoculation experiments, the results of which are summarized in table IV, were made with spores taken from the leaves of volunteer wheat collected in late fall and winter.

Seedlings grown in flower pots were exclusively used for inoculation with Septoria tritici. Following inoculation the bags were placed over the pots for three days, but were removed temporarily each day to atomize the leaves with water. On the fifth to sixth day yellow spots began to appear on the leaves of wheat. These spots enlarged and coalesced until half or more than half of the blades were yellow and drooping. Unless the plants in the greenhouse were covered with the bags for a second period or set in a large moist chamber, the yellow blades would dry and

no pycnidia would develop. The first pycnidia were observed on the twelfth day, and were distributed in greenish "islands" of tissue, which fact showed that the yellowing of the entire leaf surface was not all directly due to the attack of the *Septoria*.

That the *Septoria* of wheat under consideration is limited in its host range to the varieties of *Triticum vulgare* appears conclusive from the results of the infection experiments given in table IV. In some instances, especially with the other species of *Triticum*, and barley, oats, and rye, there was blanching of the inoculated leaves, but this progressed uniformly backward from the leaf tips and was not due to a parasite. This reaction was also subsequent to the appearance of the irregular yellow spots on the leaves of *Triticum vulgare*. No pycnidia were ever detected upon any plant except upon those in which positive infection is recorded. It is interesting to note that the fungus could not infect hosts closely allied to *Triticum vulgare* such as *T. durum*, *T. compactum*, and *T. dicoccum*. If the forms of *Septoria* upon the species of Gramineae listed below are all morphologically alike, as there is reason to believe, it is evident that *Septoria tritici* consists of more than one, possibly several biologic forms. To determine the infection-powers of the form on each of these grasses presents a profitable field for further experiment.

The frequent occurrence of this *Septoria* on the dead or over-wintering leaves of wheat suggests that it may be more saprophytic than parasitic in its habits, but the narrow limits of host range indicates a parasitic nature. If it were saprophytic it should have shown a disposition to attack the leaves of the other

cereals under the warm and moist conditions provided in the experiments, especially after the plants had become weakened.

Hosts reported for
Septoria graminum

Triticum vulgare
Hordeum vulgare
Avena sativa
Secale cereale
Poa annua
Poa compressa
Poa pratensis
Bromus sterilis
Calamagrostis epigeios
Calamagrostis langsdorfii
Digitaria sanguinale
Panicum scribnerianum
Paspalum orbiculare
Alopecurus agrestis
Avena planiculmis
Carex riparia

Hosts reported for
Septoria tritici

Triticum vulgare
Triticum caninum
Glyceria fluitans
Brachypodium
Festuca

Two series of inoculations were conducted to ascertain whether there was any variation in susceptibility among the varieties of Triticum vulgare. In the first series Turkey Red, Minnesota Reliable, Red Cross, Red Hussar, and Home Grown Spring were about equally infected. Pesterboden and Malakoff were infected to a less degree than the above varieties, while Hungarian was but slightly attacked. In the second series the more detailed data at the end of table IV were recorded. In terms of percentage Turkey Red and Beloglina each gave about 52 % infection if the leaves that had one or more spots of infection were counted. Pesterboden and Malakoff gave 43 % and Hungarian only 25 %. This is not a correct basis of comparison, however, for the individual leaves of Turkey Red and Beloglina had the largest and most numerous spots with pycnidia in the greatest number. In Hungarian often but two or three pycnidia were present on a leaf, while with Pesterboden and Malakoff the case was intermediate.

VIII Septoria malvicola F. & M.

A Septoria determined as Septoria malvicola F. & M. was collected upon Malva rotundifolia near Hutchinson, Minn. The common mallow is the only host reported for this fungus. The fact that this Septoria gave almost 100% infection (Table V) when transferred to Althaea rosea, the hollyhock, suggests that the fungus may be identical with Septoria fairmani E. & M. described on this plant. The identity appears evident when the spot characters produced upon the hollyhock by the mallow Septoria are compared with those of S. fairmani as described and as found in exsiccati. The spots on the mallow are smaller and are commonly surrounded by a broad yellow zone. When the fungus was transferred to the hollyhock, this yellow zone did not appear, but instead only the narrow black border, coincident with the limiting leaf veins was present, features given for S. fairmani. When these spots obtained by the inoculation of the hollyhock were compared with S. fairmani, "North American Fungi" No. 3557, there was agreement in all essential points. In the morphology of the fungi the specimens showed no distinctions beyond the limits of variation, and the morphological differences given in the literature are within the range of personal error. The ease with which the fungus passed from the mallow to the hollyhock indicates that this may happen in nature. The plants inoculated in the open were somewhat shaded, and were covered three days with a bell jar. The evidence is sufficient to prove the identity of S. malvicola and S. fairmani. Leaves of both Althaea rosea and Malva rotundifolia infected by inoculation with spores from the latter host are illustrated in Plate I, Figures 5 and 6.

Table V

Infections with Septoria malvicola E. & M.
from Malva rotundifolia

Date	Condi- tions	Plants inoculated	No. of leaves infected & inoculated	Remarks
Aug. 24	f-b 3	Malva rotundifolia	9/12	Check, many spots
" "	f-b 3	Althaea rosea	8/8	Spots like those of the Septoria commonly seen on the hollyhock
" "	f-b 0	Abutilon theophrasti	0/6	
" "	g-b 4	" "	0/4	
			0/10	
" "	f-b 4	Hibiscus syriacus	0/7	
Mar. 2	g-b 4	Malva rotundifolia	10/15	Oldest leaves first and most heavily infected
" "	g-b 4	Althaea rosea	6/7	

Table VI

Infections with Septoria scrophulariae Pk.

from Scrophularia marilandica

Feb. 12	g-b 3	Scrophularia marilandica	5/5	Check, many spots in 10 days
" "	g-b 4	Verbascum thapsus	3/5	Twenty spots in 18 days, no pycnidia
" "	g-b 4	Verbascum blattaria	0/10	A few spots in three weeks, prob- ably due to S. verbascicola
" "	g-b 4	Antirrhinum majus	0/10	
" "	g-b 4	Verbena urticifolia	0/10	Some minute brown spots
" "	g-b 4	Verbena hastata	0/10	Some minute brown spots
" "	g-b 4	Linaria vulgaris	0/20	

IX Septoria scrophulariae Peck

Verbascum thapsus was the only host outside the genus Scrophularia to which Septoria scrophulariae would transfer, and in this case spots without pycnidia developed. These spots are believed to represent a real cross-infection since the spores applied were from a pure culture, and the disease was confined to the area inoculated on each leaf. There is no proof that this Septoria does not also attack V. blattaria, but if this host is susceptible, the degree of susceptibility is very slight. The plants of V. blattaria transplanted from the field could not be completely freed of S. verbascicola, and this parasite continued to appear to vitiate the results of certain experiments. Whether the delayed development of a few Septoria spots on V. blattaria was due to S. verbascicola from this extraneous source or to spores of S. scrophulariae applied in inoculation could not be easily determined.

A resemblance in many respects between S. scrophulariae and S. verbascicola will be discussed in a following section.

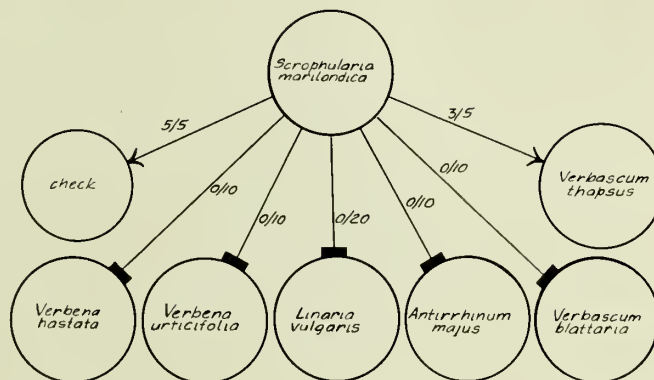


Diagram V. Infections with Septoria scrophulariae from Scrophularia marilandica

X Septoria convolvuli Desm.Septoria septulata sp. nov.

In the Saccardian description of Septoria convolvuli Desm. both Convolvulus arvensis and C. sepium are given as hosts, but the following distinctions in morphology are noted in the forms from the respective hosts: "In forma Conv. arvensis observavi sporulas 35-50 x 1-1.5, aciculares minutissime 5-6 guttulas v. septulatas hyalinas; in forma Calystegiae sporulas 35-40 x 1-1.5, continuas, hyalinas utrinque obtusiusculas. An differentiae constantes"? (Saccardo 3, p 536).

The forms of Septoria collected at Urbana upon C. arvensis and C. sepium fitted respectively the characterizations of the above forms as quoted. One hundred spores from C. arvensis had an average length of 44 microns, whereas a like number of spores from C. sepium averaged only 35.5 microns. There was a difference in average spore length whatever the conditions under which the two forms were compared. The distinction mentioned regarding spore tips is not evident, but the spores from C. arvensis were always the more definitely septate. With respect to host characters there is little by which the forms can be distinguished.

The results of the infection experiments (tables VII and VIII) proved that the forms of Septoria from these two bindweeds are likewise distinct in their powers of infections, for each can cause vigorous infection upon only its original host. The fungus from C. arvensis does infect C. sepium to some degree, with 9 out of 39 leaves inoculated showing a few small disease spots, but this is to be compared with 39 out of 45 leaves upon the original host, on which the spots were ordinarily so numerous and so spreading that

TABLE VII

Infections with Septoria septulata sp. nov.
from Convolvulus arvensis

Date	Condi- tions	Plants inoculated	No. leaves infected & inoculated	No. of spots	Remarks
Oct. 22	g-b 3	Convolvulus arvensis	15/20	many	Check, most of the leaves killed
Nov. 14	g-b 3	" "	4/5	"	
Mar. 2	g-b 3	" "	20/20 <u>39/45</u>	"	
June 26	g-b 0	Convolvulus sepium	3/20	11	Pycnidia and spores but spots very small
Oct. 22	g-b 3	" "	3/3	12	
Nov. 14	g-b 3	" "	2/7	5	
Mar. 18	g-b 4	" "	1/9 <u>9/39</u>	1 <u>29</u>	
Nov. 14	g-b 3	Ipomoea purpurea	0/5		
Mar. 2	g-b 3	" "	0/10 <u>0/15</u>		
Oct. 22	g-b 3	Ipomoea batatas	0/10		
Nov. 14	g-b 3	" "	0/7 <u>0/17</u>		
Mar. 2	g-b 4	Ipomoea learii	0/10		
Mar. 2	g-b 4	Ipomoea setosa	0/4		

TABLE VIII

Infections with Septoria convolvuli Desm.
from Convolvulus sepium

Sept. 10	f-b 4	Convolvulus sepium	6/7	21	Check, spots large
Oct. 10	g-b 4	" "	5/5	12	
Nov. 14	g-b 4	" "	5/6	16	
Mar. 18	g-b 4	" "	1/5 <u>17/23</u>	4 <u>53</u>	
Sept. 10	f-b 4	Convolvulus arvensis	0/7		Few minute spots no pycnidia, in- fection doubt- ful
Sept. 25	f-b 4	" "	0/12		
Nov. 14	g-b 4	" "	0/25		
Mar. 18	g-b 3	" "	0/35 <u>0/79</u>		
Nov. 14	g-b 4	Ipomoea purpurea	0/5		
Mar. 18	g-b 4	" "	0/5 <u>0/10</u>		
Oct. 22	g-b 4	Ipomoea batatas	0/5		
Nov. 14	g-b 4	" "	0/10 <u>0/15</u>		
Mar. 18	g-b 4	Ipomoea learii	0/20		
Mar. 18	g-b 4	Ipomoea setosa	0/5		

the leaves were entirely killed. When C. arvensis was inoculated with the fungus from C. sepium no disease spots with pycnidia were obtained upon any of 79 leaves inoculated, although minute brown spots, usually less than 1 mm. broad, were often formed. The significance of these spots is unexplained, though they may represent incipient infection.

Septoria convolvuli is reported upon Ipomoea purpurea, but all attempts to infect species of Ipomoea were futile.

Were the two forms of Septoria under consideration to be accepted as belonging to a single species, here would be a well established case of biologic specialization. But since the forms have been proved to be different both morphologically and biologically, they should each have specific rank. The name S. convolvuli is reserved for the form on C. sepium upon which host the type of S. convolvuli was described (6). For the form upon C. arvensis the following new species is proposed:

Septoria septulata sp. nov.

Spots orbicular, then irregular and confluent, light to dark brown; pycnidia mostly epiphyllous innate, globose, 60-90 μ , protruding with a prominent ostiole, 20-30 μ ; spores curved or flexuous, one end narrow with a more acute tip, 3-5 septate, 30-50 μ long by 1-2 μ wide. Habitat: old or fading leaves of C. arvensis.

This species appears to be the equivalent of the form on C. arvensis described in Saccardo's "Sylloge Fungorum", Vol. 3, p 536.

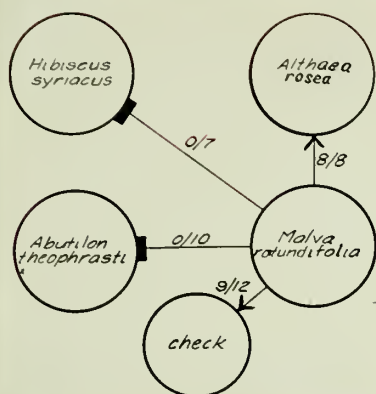


Diagram VI. Infections with Septoria malvicola from Malva rotundifolia

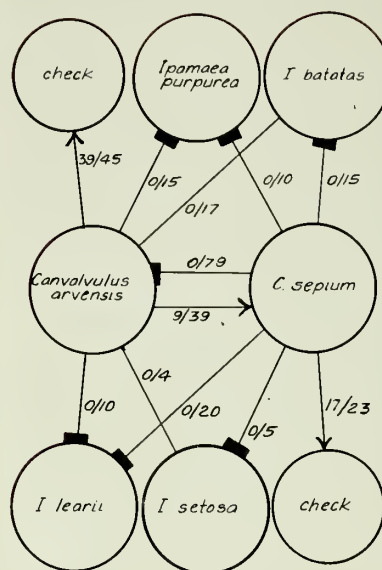


Diagram VII. Infections with Septoria septulata from Convolvulus arvensis and S. convolvuli from C. sepium

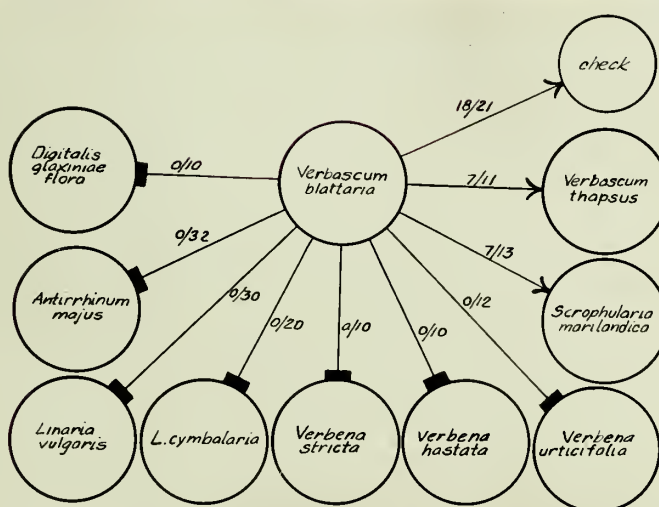


Diagram VIII. Infections with Septoria verbascicola from Verbascum blattaria

XI Septoria verbascicola B. & C.

Septoria verbascicola appears to be somewhat adaptive in its host relations. The infection of Scrophularia marilandica was as vigorous as that on the original host when conditions were made favorable for the fungus. This was done by keeping the inoculated plant constantly covered with a bell jar for ten days, and by atomizing the leaves daily with water following the application of the spores. At the end of this period under cover disease spots began to appear. The plant used was a small shoot which sprang from underground parts transplanted from a woodland in fall. It seemed to retain its full vigor notwithstanding the rather unusual conditions provided in the experiment. As may be seen from Table IX the infection of Scrophularia marilandica secured without these special conditions was slight. When the fungus was transferred back to Verbascum blattaria, the original host, there was heavy infection, though the inoculated plant was inclosed no more than two days.

The disease spots formed upon Scrophularia marilandica were essentially like those upon Verbascum blattaria. Upon either host the central area of the spots was ashen in color, while the border was reddish-brown to purplish. Under humid conditions a dull green zone appeared outside the reddish-brown ring, indicating the destruction of new tissue by the encroaching fungus, or the entire area of the spot would be dull green to black. This latter phenomenon was to be seen chiefly upon the original host. Pycnidia were numerous upon both hosts under the humid conditions.

Septoria scrophulariae Pk., which is common upon Scrophularia marilandica in nature, forms spots scarcely distinguishable from

those above described. The most important distinction is the scanty number of pycnidia; not more than a half dozen are often to be seen in a spot. The spores and pycnidia of S. verbascicola and S. scrophulariae from material collected near Urbana were so similar that it was suspected that the forms were identical. The fact that the former infected Scrophularia marilandica readily made such identity probable, but this view was shown to be questionable when it was found that the latter infected V. blattaria slightly if at all. It was discovered, moreover, that the two fungi can be separated easily in culture, as S. verbascicola produced pycnidia and spores upon all media used, while S. scrophulariae seldom did; the growth of the first was chocolate colored, that of the second buff.

Septoria verbascicola attacked V. thapsus readily, but few spore-bearing structures developed. The spots attained a size as great as those upon V. blattaria, were angular in outline, and purplish in appearance. It seems probable that this host is infected in the field, although no proof of this was secured. Leaves of mullein were collected with similar disease spots, some of which were very large but, as no pycnidia were found, it cannot be stated that the injury was caused by Septoria.

The rather constant formation of small brownish spots upon the species of Verbena following inoculation with S. verbascicola would appear to indicate incipient infection, yet the failure to obtain pycnidia, and to prove that the spots were not due to other causes leaves the matter in doubt.

Infections with Septoria verbascicola B. & C.
from Verbascum blattaria

Date	Condi- tions	Plants inoculated	No. leaves infected & inoculated	No. of spots	Remarks
Aug. 30	f-b 4	Verbascum blattaria	3/6	8	Check
Oct. 30	g-b 3	" "	5/5	43	"
Feb. 12	g-b 3	" "	10/10	75	"
			<u>18/21</u>	<u>126</u>	
Aug. 30	f-b 3	Verbascum thapsus	3/5	8	Pycnidia & spores
Oct. 30	g-b 3	" "	4/6	10	" " "
			<u>7/11</u>	<u>18</u>	
Oct. 30	g-b 3	Scrophularia mari-	2/8	5	Pycnidia & spores
Jan. 15	g-b 10	" landica	5/5	33	" " "
		" "	<u>7/13</u>	<u>38</u>	
Oct. 30	g-b 3	Verbena urticifolia	0/7	few	Infection doubtful
Feb. 12	g-b 6	" "	0/5	few	" "
			<u>0/12</u>		
Oct. 14	g-b 3	Verbena hastata	0/5	few	No pycnidia, in-
Feb. 12	g-b 5	" "	0/5	few	fection doubtful
			<u>0/10</u>		
Aug. 30	g-b 4	Verbena stricta	0/10		
Mar. 15	g-b 3	Linaria cymbalaria	0/20		
Aug. 30	f-b 0	Linaria vulgaris	0/30		
Aug. 30	g-b 3	Antirrhinum majus	0/12		
Jan. 15	g-b 3	" "	0/10		
Feb. 12	g-b 5	" "	0/10		
			<u>0/32</u>		
Mar. 15	g-b 4	Digitalis gloxini- aeiflora	0/10		

XII Septoria cirsii Niessl.

Upon Cirsium arvense, Septoria cirsii is an active parasite, both in the field and when brought into the greenhouse. In the field it attacks chiefly the lower leaves, and causes large, usually irregular, brown, dry spots, mostly along the leaf margins, but often the whole leaf is involved. In the greenhouse growth is similar but more rapid and extensive. Inoculated leaves are generally completely destroyed. The fungus is also reported upon Cirsium discolor.

According to the infection experiments conducted Septoria cirsii can make a weak attack upon both Cirsium discolor and C. lanceolatum. The spots formed upon these hosts resemble those upon C. arvense, but are smaller and very few in number. The difference in the vigor of attack upon these hosts is also well demonstrated by the length of the incubation period and the rate of development. Upon Cirsium arvense spots appeared in thirteen days after inoculation, pycnidia were observed in fifteen days, and in four weeks the whole plant was dead from the spread of the disease. Upon Cirsium lanceolatum spots were first visible in twenty days, and in four weeks they had attained a breadth ranging from 3-8 mm. Pycnidia and spores were found at this time. The plant had to be kept in a moist atmosphere to bring about the formation of many spores. The incubation period and rate of development were similar in Cirsium discolor. There were no noticeable differences in the morphology of the fungus upon the various hosts.

The relation of maturity of the spores to the presence of septa was often noticed in this species. Where spores were made to

Table X

Infections with Septoria cirsii Niessl.from Cirsium arvense

Date	Condi- tions	Plants inoculated	No. of leaves infected & inoculated	No. of spots	Remarks
June 28	f-b 0	Cirsium arvense	5/5	many	Check, leaves killed
Oct. 24	g-b 3	" "	5/5	"	" " "
Feb. 12	g-b 4	" "	15/15	"	" " "
			25/25		
June 28	g-b 0	Cirsium lanceola-	0/5		
Oct. 24	g-b 3	" " tum	1/5	4	Pycnidia & spores
Feb. 12	g-b 5	" "	3/8	8	" " "
			4/18	12	
June 28	g-b 3	Cirsium discolor	0/10		
Oct. 24	g-b 5	" "	2/10	3	Pycnidia & spores
Feb. 12	g-b 5	" "	0/10		
			2/30		
Aug. 30	f-b 0	Cirsium hilli	0/5		
Oct. 24	g-b 4	" "	0/15		
Feb. 12	g-b 4	" "	0/10		
			0/30		

Table XI

Infections with Septoria brunellae F. & H.from Prunella vulgaris

Sept. 5	f-b 0	Prunella vulgaris	3/8	8	Check
Mar. 9	g-b 4	" "	5/15	11	
			8/23	19	
Sept. 5	f-b 0	Nepeta cataria	0/5		
Mar. 9	g-b 4	" "	0/10		
			0/15		
Sept. 5	f-b 0	Nepeta hederacea	0/10		Plants shaded
Sept. 5	f-b 0	Monarda fistulosa	0/10		Plants shaded
Sept. 5	f-b 0	Blephilia hirsuta	0/5		Plants shaded
Mar. 9	g-b 5	" "	0/10		
			0/15		
Mar. 9	g-b 4	Salvia coccinea	0/10		

develop abundantly in a moist chamber, septa could not be seen at all, or could be seen only faintly after staining with iodine. In old spots or where the growth had been slow, the septa were plainly seen. Spores obtained from an old culture upon corn meal agar had septa that were strikingly definite. Plants inoculated with spores from this culture were heavily infected.

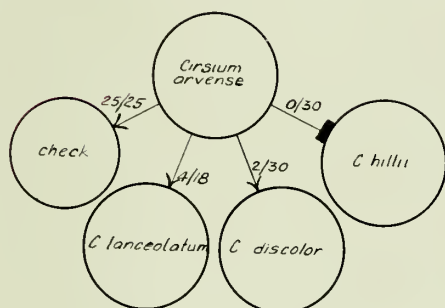


Diagram IX. Infections with Septoria cirsii from Cirsium arvense.

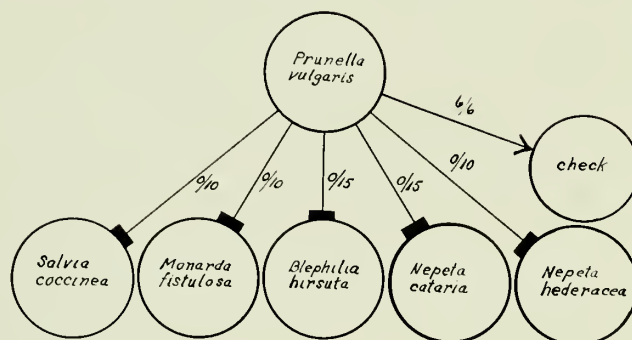


Diagram X. Infections with Septoria brunellae from Prunella vulgaris.

XIII Septoria brunellae E. & M.

The inoculations with Septoria brunellae gave negative results in all cases except upon the original host, which facts indicate that the fungus is probably limited to Prunella vulgaris in its host range. Upon this one host it is a marked parasite; frequently the whole surface of some leaves is discolored by the confluent spots.

XIV Septoria lycopersici Speg.

The inoculations with Septoria lycopersici gave results in agreement with those published by Norton (22) who inoculated several plants related to the tomato in humid inclosures. He states that spots developed better and spores ^{were} larger on potato and Solanum carolinense than on tomato, while on Datura the spots were slow growing, light colored, and small-spored. In the present experiments the spots on potato were darker in color and smaller than those on tomato, while those on Solanum carolinense were likewise darker in color, but larger, and often coalesced until the leaves were destroyed. The spots on Datura were very similar to those described by Norton. Spores developed upon the potato and Solanum carolinense produced full infection of tomato leaves.

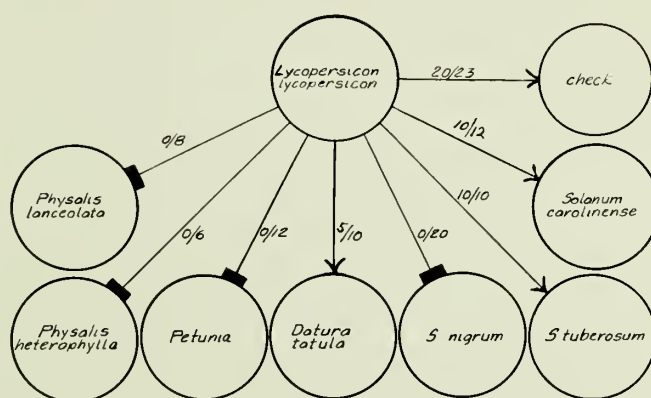


Diagram XI. Infections with Septoria lycopersici from tomato.

Table XII

Infections with Septoria lycopersici Speg. from Tomato

Date	Condi- tions	Plants inoculated	No. of leaves infected & inoculated	No. of spots	Remarks
Sept. 16	g-b 2	Tomato	5/5	30	Check
" "	g-b 2	Solanum tuberosum	0/5		Minute spots, possibly infection
" "	g-b 2	Solanum carolinense	0/5		Minute spots, possibly infection
" "	g-b 2	Solanum nigrum	0/5		
" "	g-b 2	Datura tatula	0/5		
" "	g-b 2	Physalis heterophyl- la	0/6		
" "	g-b 2	Physalis lanceolata	0/8		
Mar. 2	g-b 3	Tomato	10/13	many	Check, leaves
" 18	g-b 5	"	10/10	"	killed
			<u>20/23</u>		
" 2	g-b 5	Solanum tuberosum	10/10	many	Pycnidia & spores
" 2	g-b 5	Solanum carolinense	4/4	many	Pycnidia & spores
" 18	g-b 5	" "	6/8	"	" " "
			<u>10/12</u>		
" 18	g-b 5	Datura tatula	5/10	24	Few pycnidia and spores
" 18	g-b 5	Solanum nigrum	0/20		Few yellowish, possibly infection
" 18	g-b 7	Petunia	0/12		

XV Septoria lepidiicola F. & M.

Septoria lepidiicola is reported upon only Lepidium virginicum and L. apetalum. The data in table XIII show that the fungus on these two hosts is identical biologically as well as morphologically. The negative results obtained when plants belonging to other genera of Cruciferae were inoculated indicate that the fungus is confined to the species of Lepidium. No data are at hand to show whether it will attack more than the two species of the genus. The failure to obtain signs of incipient infection, such as spots without spore-bearing-bodies, upon species outside the genus Lepidium proves that the fungus has little adaptability. It may be possible, however, to obtain growth in some form upon the remaining species of Lepidium that have not been inoculated experimentally.

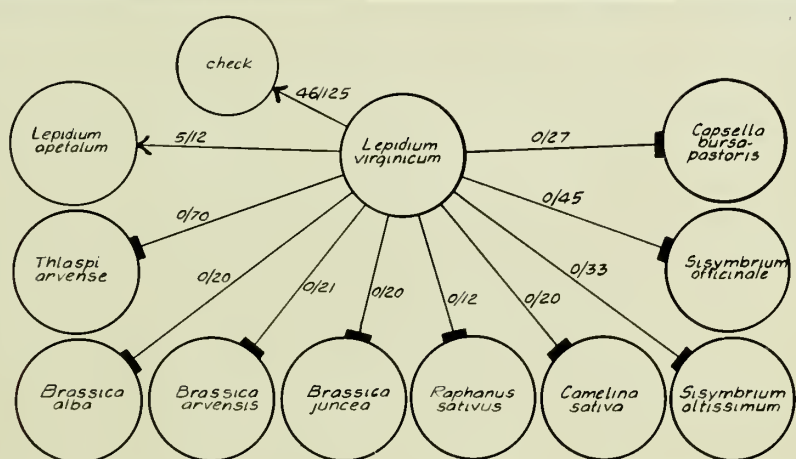


Diagram XII. Infections with Septoria lepidiicola from Lepidium virginicum.

Table XIII

Infections with Septoria lepidiicola E. & M.
from Lepidium virginicum

Date	Condi- tions	Plants inoculated	No. of leaves infected & inoculated	Check infections on original host
June 6	g-b 3	Lepidium apetalum	5/12	7/20
Oct. 12	g-b 4	Thlaspi arvense	0/30	8/25
Oct. 23	g-b 4	" "	0/40	11/40
			0/70	19/65
Mar. 6	g-b 3	Brassica alba	0/20	20/40
Mar. 6	g-b 3	Brassica arvensis	0/10	20/40
June 6	g-b 3	" "	0/11	7/20
			0/21	27/60
Mar. 6	g-b 3	Brassica juncea	0/20	20/40
Mar. 6	g-b 3	Raphanus sativus	0/5	20/40
June 6	g-b 3	" "	0/7	7/20
			0/12	27/60
Mar. 6	g-b 3	Camelina sativa	0/20	20/40
Oct. 23	g-b 4	Sisymbrium altissimum	0/33	11/40
Mar. 6	g-b 3	Sisymbrium officinale	0/15	20/40
June 6	g-b 3	" "	0/10	7/20
Oct. 23	g-b 4	" "	0/20	11/40
			0/45	38/100
June 6	g-b 3	Capsella bursa-pas-	0/7	7/20
Oct. 23	g-b 3	" " toris	0/20	11/40
			0/27	18/60

XVI Septoria helianthi Ell. & Kell.

The following plants have been reported as hosts for Septoria helianthi:

- | | |
|-------------------------------------|---------------------------------|
| 1. <u>Helianthus grosseserratus</u> | 5. <u>Helianthus petiolaris</u> |
| 2. " <u>annuus</u> | 6. " <u>lenticularis</u> |
| 3. " <u>doronicoides</u> | 7. " <u>strumosus</u> |
| 4. " <u>californicus</u> | 8. <u>Heliopsis laevis</u> |

In the vicinity of Urbana this Septoria was a common parasite of H. grosseserratus, upon the lower or shaded leaves of which it causes grayish-black spots that often become more than a centimeter in breadth. It was less commonly found upon H. tuberosus, upon which the spots are smaller, and rarely upon H. annuus and H. rigidus.

In three separate trials H. grosseserratus was readily infected with its own form of Septoria without maintaining a humid atmosphere beyond three days. The other species of Helianthus infected by the Septoria from H. grosseserratus are shown in diagram XIII. Except for H. tuberosus, which grew natively in the greenhouse yard, all these cross-infections were upon seedlings grown in the greenhouse. Proof of infection was obtained only by detaching spotted leaves and laying them in a moist chamber to induce the development of pycnidia. For this reason, as well as on account of the attack of insect pests, no accurate data could be secured concerning the degree of susceptibility of certain of the hosts, consequently some of the records are wanting. It is clear, however, that the original host is the only one that is congenial for this Septoria from H. grosseserratus, for on its own host alone spore-bearing bodies developed naturally under the ordinary greenhouse environment. The infection of small shoots of H. tuberosus covered, out of doors, with a bell jar was relatively feeble. Numerous spots developed but the

author could not satisfy himself that they were entirely due to *Septoria*, on account of the scanty appearance of pycnidia, and because a *Phyllosticta*, apparently saprophytic however, often appeared when the leaves were placed in a moist chamber.

It appears significant that the *Septoria* from *H. rigidus* did not infect *H. grosseserratus* when the plant, inoculated in the field was bagged five days, and that the form from *H. tuberosus* did not give ready infection of *H. grosseserratus* in the greenhouse. The failure of infection in the series of inoculations made upon mature plants of various species of *Helianthus* on Sept. 16 in the greenhouse (Table XIV), and also upon similar hosts in the field in summer, in which spores from *H. grosseserratus* were used, may have been due to the age of the leaves, yet the checks on the original host gave positive results. A corresponding set of hosts were inoculated at these same periods with spores from *H. tuberosus* with negative results, but these were not recorded in the table as no checks were used. Still in these cases the spores germinated well in laboratory tests.

All the data obtained respecting *Septoria helianthi* indicate that the forms used in inoculation are not vigorously parasitic except upon their original hosts. These data are scarcely ample for definite conclusions, yet the results are in harmony with what was observed regarding the host range of this *Septoria* in the vicinity of Urbana. If there are no fixed biologic forms, nevertheless there appears to be a degree of specialization upon the different species of *Helianthus*, possibly of a temporary nature such as Montemartini (18) claims for rusts.

Table XIV

Infections with Septoria helianthi Ell. & Kell.From Helianthus grosseserratus

Date	Condi- tions	Plants inoculated	No. of leaves infected & inoculated	Remarks
Sept. 16	g-b 3	<i>Helianthus grosseserratus</i>	5/5	Check, leaves mature 32 spots
" "	g-b 3	<i>Helianthus occidentalis</i>	0/6	Leaves mature
" "	g-b 3	<i>Helianthus rigidus</i>	0/5	" "
" "	g-b 3	<i>Helianthus mollis</i>	0/5	" "
" "	g-b 3	<i>Helianthus tuberosus</i>	0/5	" "
" "	g-b 3	<i>Helianthus annuus</i>	3/8	Seedlings, pycnidia in moist chamber 10 spots
" "	g-b 3	<i>Silphium integrifolium</i>	0/5	
" "	g-b 3	<i>Bidens cernua</i>	0/20	
July 5	g-b 3	<i>Helianthus grosseserratus</i>	7/7	Check, leaves young 26 spots
" "	f-b 4	<i>Helianthus tuberosus</i>	4/20	Many spots, but few with pycnidia
" "	f-b 4	<i>Helianthus mollis</i>	0/7	Leaves young
" "	f-b 4	<i>Helianthus rigidus</i>	0/10	" "
" "	f-b 4	<i>Silphium integrifolium</i>	0/5	
Jan. 5	g-b 4	<i>Helianthus rigidus</i>	plus	Seedlings, only spots formed
" "	g-b 4	<i>Helianthus argyrophyllus</i>	4/20	Seedlings, pycnidia in moist chamber
" "	g-b 4	<i>Helianthus cucumerifolius</i>	6/20	As above
Mar. 2	g-b 4	<i>Helianthus grosseserratus</i>	plus	Check, seedlings
" "	g-b 4	<i>Helianthus californicus</i>	plus	Seedlings, pycnidia in moist chamber

Infections with Septoria helianthi Ell. & Kell.

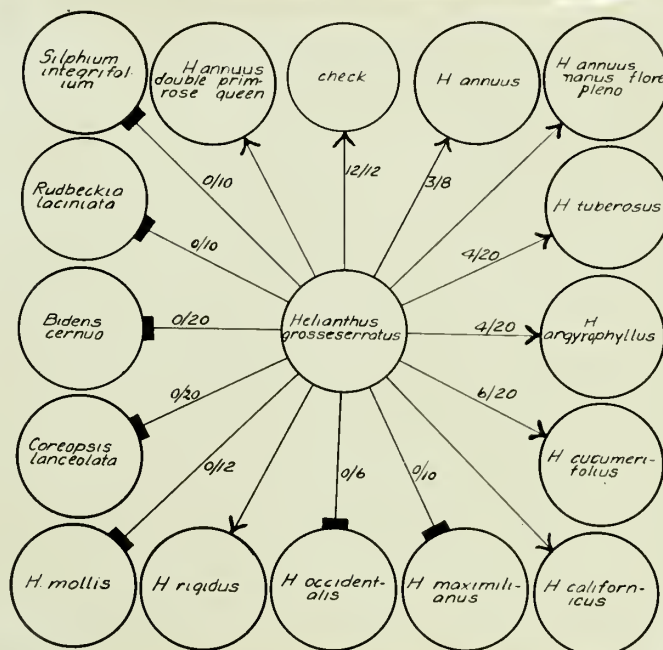
Mar. 2	g-b 4	<i>Helianthus annuus nanus flore pleno</i>	plus	Seedlings, pycnidia in moist chamber
" "	g-b 4	<i>Helianthus annuus double primrose queen</i>	plus	As above
" "	g-b 4	<i>Helianthus maximilianus</i>	0/10	
" "	g-b 4	<i>Coreopsis lanceolata</i>	0/20	
" "	g-b 4	<i>Rudbeckia laciniata</i>	0/10	

Spores from Helianthus tuberosus

July 24	f-b 4	<i>Helianthus tuberosus</i>	4/10	Check, pycnidia and spores
" "	g-b 4	<i>H. grosseserratus</i>	0/5	
" "	f-b 4	<i>Helianthus rigidus</i>	0/10	
" "	f-b 4	<i>Helianthus mollis</i>	0/10	
" "	f-b 4	<i>Helianthus annuus</i>	0/5	
" "	f-b 4	<i>Silphium integrifolium</i>	0/5	

Spores from Helianthus rigidus

Sept. 18	f-b 5	<i>H. grosseserratus</i>	0/8	No check, but spores germinated well in laboratory tests
" "	f-b 5	<i>Helianthus tuberosus</i>	0/5	

Diagram XIII. Infections with Septoria helianthi from Helianthus grosseserratus.

XVII Septoria rubi West.

Septoria rubi was collected frequently at Urbana upon Rubus occidentalis, the black raspberry, but was never found upon any species of Rubus belonging to the blackberry, or Eubatus, section of the genus. Since plants of the blackberry were often growing in close enough proximity to R. occidentalis to enable them to become inoculated with the Septoria, it appears that the species of blackberry were not susceptible to the fungus on the black raspberry. During July thirty leaves each of R. occidentalis and a species of blackberry were inoculated with spores of Septoria from the former host. Both of these plants inoculated were young, and were growing close together in a shaded place. In two weeks all the thirty leaves of R. occidentalis were thickly spotted with Septoria, but no trace of infection could be found upon the blackberry.

No definite conclusions can be drawn from the above observations, and the accompanying experiment. The facts may indicate that Septoria rubi is split into biologic forms, or that the species of blackberry in this locality are permanently resistant to the Septoria. This fungus is reported, however, upon twenty-eight or more species of Rubus, distributed among all sections of the genus, a fact that makes it appear probable that all members of the genus are parasitized. If this be true the brief data above indicate the existence of biologic forms in S. rubi. The large number of species in the genus Rubus, of which so many are known to be hosts of Septoria, makes them an attractive field for a further study of biologic specialization.

XVIII Septoria atro-purpurea Peck

The presence of disease spots without pycnidia is the only indication that Septoria atro-purpurea from Aster cordifolius can infect A. ericoides and A. laevis. This infection was obtained under prolonged humid conditions, and it is improbable that it occurs often in nature. These asters have not been reported hitherto as hosts for the fungus. This parasite, according to specimens in the Herbarium of the United States Department of Agriculture, attacks Solidago latifolia and Machaeranthera aspera. The data indicate that this Septoria is able to adapt itself to related hosts to a considerable degree.

The disease spots on A. cordifolius are nearly orbicular, with a central area of reddish-brown and a margin of light green. In the larger and older spots a gray area appears within the reddish-brown. Upon A. ericoides the spots were a bright reddish color, with a margin of yellow, and a ragged and indefinite outline. The spots on A. laevis were very small and brown, indicating that the fungus was less well adapted to this host than to A. ericoides. As the spores for inoculation were from pure culture, and adjacent leaves not inoculated showed no symptoms of disease, it appears certain that the spots in question were due to the Septoria applied.

Table XV

Infections with Septoria atro-purpurea Peck
from Aster cordifolius

Date	Condi- tions	Plants inoculated	No. leaves infected & inoculated	No. of spots	Remarks
Feb. 25	g-b 6	<u>Aster cordifolius</u>	11/18	46	Check
" "	g-b 6	<u>Aster ericoides</u>	4/10	13	No pycnidia
" "	g-b 6	<u>Aster laevis</u>	4/15	9	No pycnidia

XIX General Discussion

Age incidence. - In the field *Septoria* spots are more frequently observed upon the old or fading leaves of plants, but this is often due to the fact that the young leaves have recently expanded, and have not had time to become infected. The immature foliage is sometimes the more susceptible, but this varies with hosts. From the results of the infection experiments the leaves of *Lepidium virginicum* appear to be equally susceptible at all ages. Old leaves of *Lactuca scariola* in which the edges are cracked and drying are infected without difficulty, but the spots remain small. Partially grown leaves of this host are more easily infected, and the spots become larger. The older leaves of *Convolvulus arvensis* and *C. sepium* are the most heavily attacked. While inoculation of the immature leaves seldom produces infection.

The influence of age upon susceptibility is very well shown in *Malva rotundifolia* and *Althaea rosea*. Disease first develops on the oldest leaves, in those of intermediate age the incubation period has greater length, while those partially grown are resistant. A plant of *Althaea rosea* with seven leaves was thoroughly wetted with a suspension of spores of *Septoria malvicola*, and kept under a bell jar four days. In ten days the five mature leaves were spotted, the oldest having the heaviest infection. It was nearly three weeks before the sixth leaf showed disease, and the seventh or youngest leaf inoculated continued healthy. In two trials with the mallow there were similar results, which are in accord with what one sees in the field, for there only old shaded leaves are badly attacked.

Susceptibility of different leaf surfaces. - Equal areas of

the upper and lower surfaces of separate sets of leaves of a number of plants were inoculated, and other factors made as comparable as possible. In Lactuca scariola the upper surface gave the heavier infection. In Polygonum persicaria 39 spots, 1 mm. to 5 mm. in diameter, resulted on the top side against six spots, 1 mm. to 2 mm. in diameter, on the bottom. The leaf surface of Erigeron annuus in 150 separate areas, 75 above and 75 below, was inoculated with loop-drops of a suspension of spores of Septoria erigerontis, and 14 infections from above and six from below were obtained. In contrast to these experiments the inoculation of the lower surface of leaves of Solanum carolinense with S. lycopersici gave abundant infection, while leaves inoculated above remained free of disease. No explanation of the above results can now be given, but the number of stomata, the character of the cuticle, the ease with which the suspension makes contact with the surface, and the light exposure may be factors.

Effect of the mass of inoculum.- The effect of varying the concentration of the spore suspension was tested. One hundred areas upon Erigeron annuus were inoculated with loop-drops containing approximately 100 spores, and an equal number of areas with loop-drops averaging 1 to 3 spores. In the former case there were 35 areas infected, and in the latter 15, but in the 35 areas over 80 points of infection were noted, while in the 15 areas only 18 were present. Infections were obtained upon Lactuca scariola with loop-drops containing only 1 to 3 spores in 11% of the inoculations.

Effect of wounding.- Certain leaves of young potted plants of Malva rotundifolia were perforated with a fine needle in numerous places. All the leaves of each plant were inoculated over the entire

upper surface, and bagged for four days. Only the perforated leaves became infected. Either the wounding had the effect of overcoming the resistance shown to be present in the young foliage, or the pierced epidermis afforded an easy entrance for the germ tubes of the spores.

Variations in the morphology of the fungus.— The more detailed studies of morphological variations were made with Septoria tritici and S. verbascicola, and the chief results obtained are shown in graph I by curves which represent the ranges of spore length in these fungi under a number of different conditions. No investigation was made of the factors causing these variations, but apparently they are due to differences in humidity. An increase in spore length when infected leaves were kept in a moist chamber for a period was apparent in many other species of Septoria.

There was no alteration in spore length when S. verbascicola was transferred from Verbascum blattaria to Scrophularia marilandica under comparable conditions, as E and F of graph I show. Norton (22) reports that the spores of the tomato Septoria become longer upon the potato and Solanum carolinense, but shorter upon Datura tatula than they were upon the original host, when the inoculations were made within humid inclosures. It is not stated whether he took account of environmental relations other than the change of host, but the lesser spore length upon Datura tatula makes it appear that the host has a definite effect on morphology. Still in the numerous crosses recorded in the tables of the present paper, no changes of spore length were observed for which environmental factors such as humidity might not account, at least in all cases in which the fungus and host were in compatible relations.

If all the species of *Septoria* have a corresponding relation to the environment, and if all have a broad range between the maximum and minimum spore length, as in *S. tritici* and *S. verbascicola*, it is obvious that many of the measurements now given in specific descriptions are far from accurate. The range of 19 to 62 microns reported for *S. sisymbrii* is not of greater width than that shown for the fungi in graph I, and indicates care in measurement. It is not proper to compare dry herbarium specimens with material freshly collected, especially if it has been allowed to form spores in a moist chamber. It is well to make a record of the source of the material collected, and the conditions under which it was found, cf., graph I, C, D, G, and H.

Host limitations.— The experimental results thus far obtained indicate that the species of *Septoria* do not have a broad host range. Each can infect vigorously one or a few closely allied plants, and can infect to a less degree a number of hosts that stand in rather immediate relation to the vigorously infected ones. In some cases this host range does not extend beyond the limits of a genus, and in other cases includes but two or three related genera. Although some of the fungi studied have been found to have approximately the host range previously reported for them, in many instances the host ranges established by the experiments have been much more narrow than the reports on hosts would lead one to conclude, a few forms being limited to the species upon which they are collected. Notable illustrations of this are the forms of *Septoria* on wheat, *Convolvulus sepium*, and possibly upon *Rubus occidentalis* and *Helianthus* sp. Further infection experiments would doubtless reveal more cases of identity both morphologically and biologically among

forms now classed as separate species, while at the same time some of the present species would be shown to consist of more than one morphological form, or species.

The value of disease characters.- The variable nature of disease characters, as manifested by the host, has been well demonstrated. These variations are dependent upon the species, the age, and the part of the host as well as upon environmental conditions. On this account these characters lose much of their value in taxonomy, but inasmuch as the host ranges of the species of *Septoria* are not broad, and the number of forms parasitizing a single host are very few, such characters may be of some use in distinguishing the parasites on individual hosts. For these same reasons the host itself will continue to be a valuable key in the determination of the fungus.

Biologic specialization.- The experiments herein described have not been broad enough to include forms from all the hosts reported for any species, especially with such fungi as *Septoria rubi* upon numerous members of *Rubus*, *S. graminum* or *S. tritici* upon several different genera of *Gramineae*, and *S. polygonorum* on various species of *Polygonum*. Great difficulty will inevitably be met in bringing together even a major portion of the respective forms for comparative study, such as would be necessary to firmly establish the existence of biologic specialization, and to ascertain the number of biologic forms. Still such data as the present investigations furnish indicate clearly that biologic specialization exists in many species of *Septoria*. This is shown by the fact that in many instances the *Septoria* from one host either fails to infect, or infects to only a slight degree, certain hosts upon which

morphologically similar forms of *Septoria* are known. In illustration of this, the species of *Septoria* from wheat, from *Pubus occidentalis*, and from certain species of *Helianthus* and *Polygonum* furnish examples.

XX Conclusions

1. The results of the present investigations indicate that certain species of *Septoria* are differentiated into biologic forms.

2. Although some forms show a degree of adaptability in host relations, in general the species studied are limited to one or to a few closely related hosts which they can vigorously infect.

3. In some cases the host range does not extend beyond the limits of a genus, while in other cases two or three related genera are included.

4. In many cases the host ranges established by the experiments have been more narrow than the host indices indicate.

5. Disease characters, as manifested by the host, vary with the host and with environmental conditions, and are therefore unreliable in taxonomy.

6. Certain species of *Septoria* have been shown to vary considerably in morphological characters under different environmental conditions, and hence the value of measurements now given in specific descriptions is questionable.

7. Inoculation experiments show that *Septoria malvicola* F. & M. and *S. fairmani* E. & E. are identical.

8. Similar experiments show that the form of *S. convolvuli* Desm. described upon *Convolvulus arvensis* is biologically as well

as morphologically distinct from the type form of S. convolvuli described upon C. sepium, and is entitled to specific rank.

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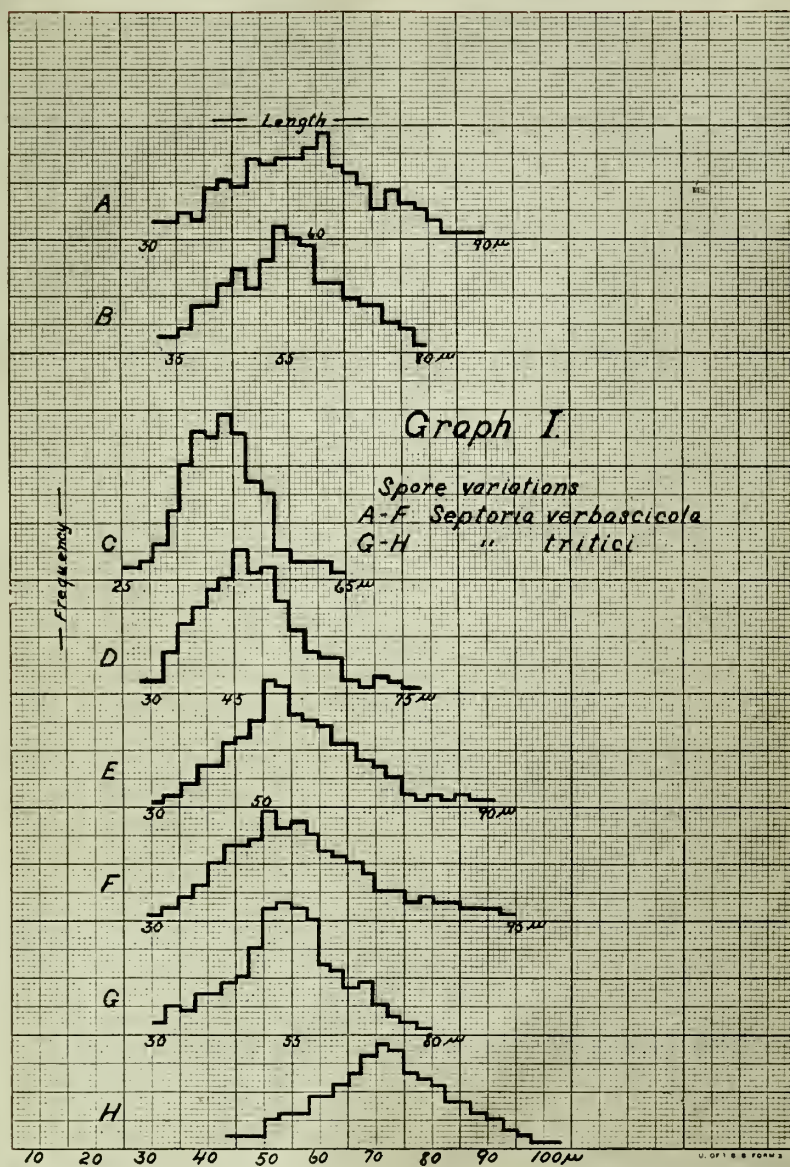
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Explanation of Graph I

This graph represents variations in spore length in Septoria verbascicola B. & C. and S. tritici Desm. under a number of different conditions. The measurements of spores are indicated in microns by the base line, each space representing one micron. The frequency is indicated on the perpendicular lines, each space representing one spore. The measurements are at intervals of 2.4 microns, and for each curve 200 spores were measured.

A and B represent ranges in length of spores from a single culture of S. verbascicola upon onion agar; in A the spores were from the lower portion of the colony which was moistened by the small amount of water on the agar, while in B the spores were from the upper edge of the colony where the agar was drying. C represents spores from spots on leaves of Verbascum blattaria in the field where the light exposure was intense; D, spores from shaded rosette leaves of the same host in the field; E, spores from the same host kept under very humid conditions in the greenhouse; F, spores of the same fungus growing upon Scrophularia marilandica, conditions as in E.

G represents the range of spore length of S. tritici upon the upper stem leaves of naturally infected wheat plants in the field in July; H, spores of the fungus from the same field taken from the basal leaves of volunteer wheat in January. The plants of wheat were dug up and kept for a few days in a closed collecting can in the greenhouse in the latter instance.



Explanation of Plate I

Fig. 1 Disease spots of Septoria polygonorum Desm. upon Polygonum pennsylvanicum. Natural infection.

Fig. 2 Disease spots of the same fungus upon P. persicaria. Natural infection.

Fig. 3 Disease spots of the same fungus upon P. lapathifolium. Natural infection.

Fig. 4 Disease spots of the same fungus upon P. orientale. Artificial inoculation.

Fig. 5. Disease spots of S. malvicola E. & M. upon Malva rotundifolia. Artificial inoculation.

Fig. 6 Disease spots of S. malvicola upon Althaea rosea. Inoculated with spores from M. rotundifolia.

Fig. 7 Disease spots of S. lactucicola E. & M. upon Lactuca scariola. Inoculated with spores from L. canadensis.

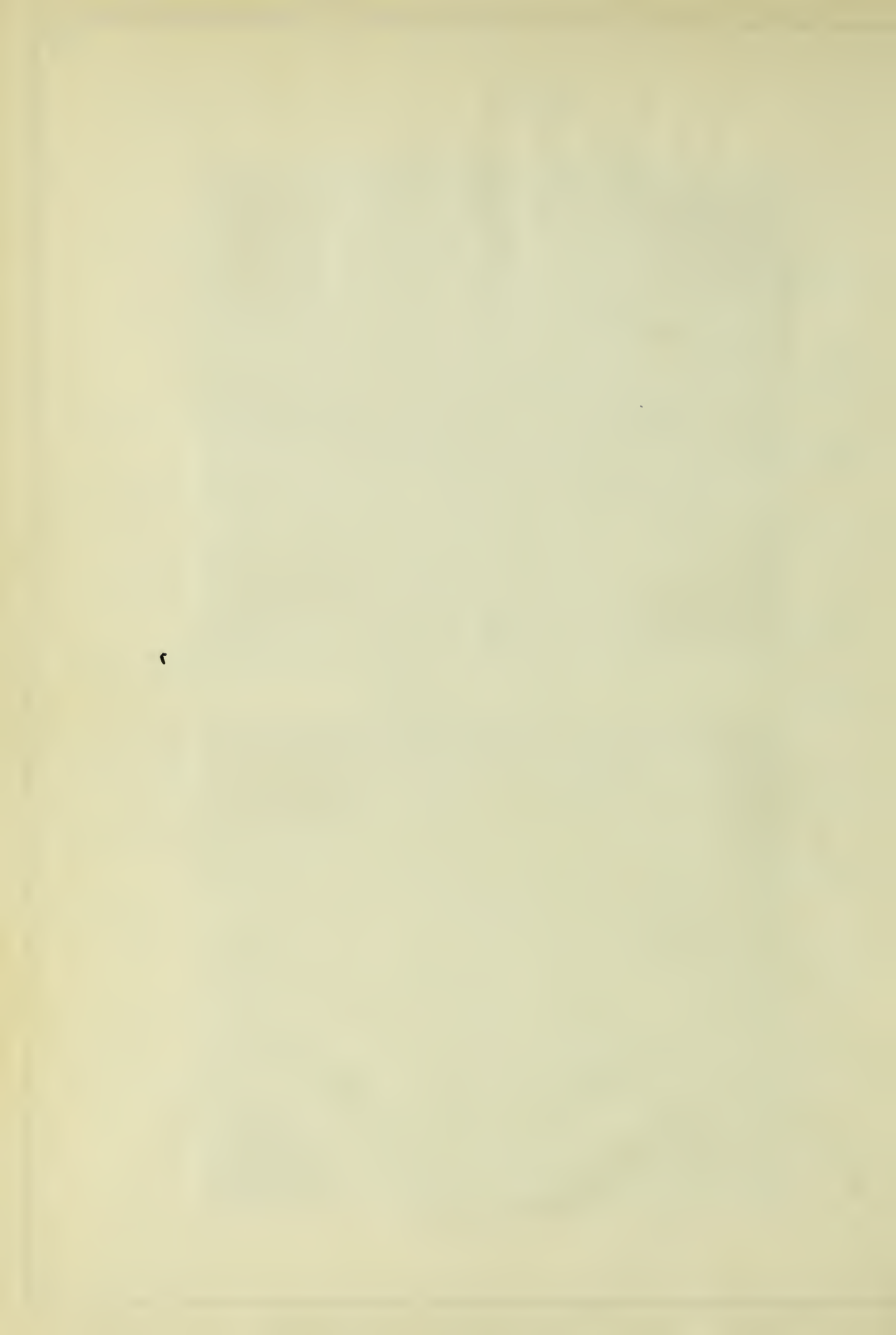
Fig. 8 Disease spots of S. lactucicola upon L. sativa. Inoculated with spores from L. canadensis.

Fig. 9 Disease spots of S. lactucicola upon L. canadensis. Natural infection.

Preparatory to photographing the leaves were treated with hot alcohol to remove the chlorophyll, but this process produced no apparent change in the character of the disease spots. The leaves were then softened in 50% glycerine and pressed.

Plate 1



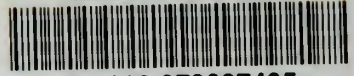


The writer takes pleasure in making acknowledgement to Dr. F.L. Stevens, Professor of Plant Pathology, University of Illinois, for helpful suggestions and guidance in the preparation of this thesis. The writer also wishes to express his appreciation of the valuable assistance given by Prof. William Trelease, Head of the Department of Botany, University of Illinois, in the solution of questions of taxonomy. Thanks are due Fred G. Seaver, Curator at the New York Botanical Garden, and Vera K. Charles, Mycologist, U.S. Dept. of Agriculture, for furnishing data upon the host ranges of various species of Septoria.

Biographical Sketch

Walter Spurgeon Beach was born near Brownton, Minnesota, January 24, 1890. He attended the Hutchinson High School, Minnesota, and graduated in 1907. The three following years were devoted to teaching in the rural schools of McLeod County of the said state. In 1910 he entered the Minnesota Agricultural College and in 1914 received the degree of Bachelor of Science in Agriculture. During the last two years of his college course he taught as a student assistant in Botany. In 1914 he accepted a position as a teaching fellow in plant pathology at the Michigan Agricultural College and received the degree of Master of Science in 1915. The Master's thesis entitled "The Fusarium Wilt of the China Aster" was approved for a technical bulletin by the Michigan Agricultural College. In the fall of 1915 he took a position as Assistant in Botany at the University of Illinois, and began study in the pursuit of the degree of Doctor of Philosophy. In 1917 he was elected to the chapter of Sigma Xi at the University of Illinois. In the college year 1917-1918 he was a fellow in Botany at the University of Illinois.

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